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Dispersal in dendritic networks: Ecological consequences on the spatial distribution of population densities

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Abstract

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2. Much of the previous work on ecological and evolutionary dynamics in metapopulations and metacommunities in dendritic river networks has been either using comparative approaches or was purely theoretical. However, the use of microcosm experiments provides the unique opportunity to study large-scale questions in a causal and experimental framework.
3. We conducted replicated microcosm experiments, in which we manipulated the spatially explicit network configuration of a landscape and addressed how linear versus dendritic connectivity affects population dynamics, specifically the spatial distribution of population densities, and movement behaviour of the protist model organism *Tetrahymena pyriformis*. We tracked population densities and individual-level movement behaviour of thousands of individuals over time.
4. At the end of the experiment, we found more variable population densities between patches in dendritic networks compared to linear networks, as predicted by theory. Specifically, in dendritic networks, population densities were higher at nodes that connected to headwaters compared to the headwaters themselves and to more central nodes in the network. These differences follow theoretical predictions and emerged from the different network topologies per se. These differences in population densities emerged despite weakly density-dependent movement.
5. We show that differences in network structure alone can cause characteristic spatial variation in population densities. While such differences have been postulated by theoretical work and are the underlying precondition for differential dispersal evolution in heterogeneous networks, our results may be the first experimental demonstration thereof. Furthermore, these population-level dynamics may affect extinction risks and can upscale to previously shown metacommunity level diversity dynamics. Given that many species in natural river systems exhibit strong spatiotemporal patterns in population densities, our work suggests that abundance patterns should not only be addressed from a local

environmental perspective, but may be the outcome of processes that are inherently driven by the respective habitat network structure.

KEYWORDS

bacteria–protist metacommunities, dispersal, ecological theory, microcosm experiment, protists, river-like networks

1 | INTRODUCTION

An extensive part of classic theoretical and empirical ecology has focused on localised and well-mixed populations or communities. However, in most natural systems, populations and communities are heterogeneous and spatially structured with dispersal connecting patches across space. The spatial structure and dynamics across multiple populations or communities may strongly affect local dynamics, and the study of spatial dynamics has more recently become a central theme in ecology (Hanski, 1999; Leibold et al., 2004).

Spatial dynamics are likely relevant and occurring in all ecosystems and habitat types, but may be especially prevalent in some ecosystems due to specific intrinsic geophysical structures. River networks may be the most prominent example thereof (Altermatt, 2013; Brown & Swan, 2010; Grant, Lowe & Fagan, 2007; Peterson et al., 2013). Rivers and river networks are shaped by very general geological processes (Rodríguez-Iturbe & Rinaldo, 1997), which result in characteristic and universal spatial network structures. The significance of spatial dynamics in these fractal, dendritic networks has received much interest over the last years (e.g. Carrara, Altermatt, Rodríguez-Iturbe & Rinaldo, 2012; Grant et al., 2007; Mari, Casagrandi, Bertuzzo, Rinaldo & Gatto, 2014; Muneeppeerakul et al., 2008; Peterson et al., 2013; Seymour, Fronhofer & Altermatt, 2015) due to the universality of the spatial network, often defining dispersal pathways, and due to the exceptionally high diversity found in natural river systems (Dudgeon et al., 2006; Vorosmarty et al., 2010). Furthermore, in many natural river systems both the network structure and the biological communities are currently rapidly changing due to habitat modifications, building of dams across waterways or species invasions (Lynch et al., 2011; Vorosmarty et al., 2010). This creates an immediate need for a better understanding of how river and river-analogue network structures drive population and community dynamics.

Extensive previous work addressing ecological and evolutionary dynamics in dendritic river networks has been either using comparative approaches or was purely theoretical. Empirical studies have for example documented that local habitat conditions and network position affect the composition of local communities and abundances of organisms (e.g. Altermatt, Seymour & Martinez, 2013; Heino, Muotka & Paavola, 2003; Heino et al., 2015; Liu, Soininen, Han & Declerck, 2013; Tonkin, 2014). Theoretical studies have been extensively addressing how network structure and dispersal along the specific network configuration drive

metacommunity composition and biodiversity (e.g. Fagan, Grant, Lynch & Unmack, 2009; Mari et al., 2014; Muneeppeerakul et al., 2008; Peterson et al., 2013). More recently, models have incorporated eco-evolutionary dynamics and feedbacks to investigate if and how river-like network structures are more likely to result in fluctuations of population densities and subsequent classic metapopulation dynamics compared to linear landscapes or other types of networks (Fronhofer & Altermatt, 2017). Such population-level fluctuations may eventually affect extinction dynamics and are thereby the underlying process shaping (meta)community structure and diversity. While both comparative and theoretical approaches are highly important, we currently lack a causal experimental breakdown of local versus regional factors driving the observed population dynamics. Microcosm experiments may fill this gap, as they offer a possibility to bridge from theoretical models to comparative field studies.

Microcosm experiments have a long tradition in ecology, and have been important in improving our understanding of predator–prey dynamics (Gause, 1934; Hiltunen, Ayan & Becks, 2015; Holyoak & Lawler, 1996), competitive interactions (Cadotte et al., 2006; Carrara, Giometto, Seymour, Rinaldo & Altermatt, 2015; Livingston et al., 2012), dispersal ecology (e.g. Cadotte et al., 2006; Jacob, Chaine, Schtickzelle, Huet & Clobert, 2015) or evolutionary dynamics (Bell & Gonzalez, 2009; Fronhofer & Altermatt, 2015; Hiltunen & Becks, 2014; Van Petegem, Boeye, Stoks & Bonte, 2016). The goal of these studies is not to give a 1:1 representation of a real ecosystem, but rather to disentangle individual driving factors in a causal approach, and to give empirical proof of principles of theoretically postulated processes (Altermatt et al., 2015; Jessup et al., 2004). Such microcosm experiments are thought to be especially advantageous in addressing questions that include otherwise (i.e. in the natural system) large spatial or temporal scales. It is thus of no surprise that microcosm experiments have recently been extensively used to address the significance of spatial dynamics on community composition and biodiversity in riverine ecosystems. Many of these studies have been giving insights into how dispersal in dendritic network structures gives rise to characteristic diversity patterns (Carrara, Rinaldo, Giometto & Altermatt, 2014; Carrara et al., 2012; Seymour & Altermatt, 2014; Seymour et al., 2015). The focus of all of these studies was at the metacommunity level and they were looking at integrative measures of biodiversity (usually number of species/ α -diversity). Thereby they largely neglected the underlying distributions and dynamics of population densities in the networks.

Importantly, the combination of all these population level demographic processes will eventually shape metacommunity composition and structure. Yet, such population dynamics in single species systems have hitherto only been studied in an invasion context in linear landscapes (Fronhofer & Altermatt, 2015; Fronhofer, Nitsche & Altermatt, 2017; Giometto, Altermatt & Rinaldo, 2017; Giometto, Rinaldo, Carrara & Altermatt, 2014).

Population level dynamics, however, are critical for population viability, conservation and evolutionary dynamics. For example, recent theoretical work shows that heterogeneity in spatial connectivity is a crucial component for the evolution of dispersal (Henriques-Silva, Boivin, Calcagno, Urban & Peres-Neto, 2015), which directly affects (meta)population level metrics such as indices of genetic population differentiations and extinction likelihoods (Fronhofer & Altermatt, 2017), and eventually also metacommunity composition. An underlying theoretical component of all these dynamics is a dependency of population sizes on network connectivity. To our knowledge, however, there is hitherto no experimental work that has assessed the effect of spatial network configurations on population density distributions and dynamics.

We used protist microcosm experiments to study the effect of spatial network configuration, specifically linear versus dendritic connectivity, on population dynamics and movement behaviour of the ciliate model organism *Tetrahymena pyriformis* kept on a bacterial resource. Using replicated multi-patch landscapes of different network configuration (Figure 1), we could assess abundance dynamics and movement behaviour of thousands of organisms over time. We show that differences in network structure alone can cause characteristic spatial variation in population densities, as predicted by simple theoretical considerations (Table 1). Our results suggest that the commonly observed strong spatiotemporal fluctuations in population densities, and eventually metacommunity structure, of many riverine organisms may not only be driven by local dynamics, but may be the outcome of processes that are inherently linked to the habitat network structure.

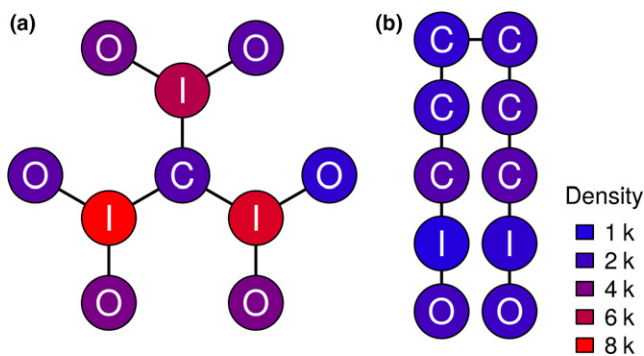


FIGURE 1 Median population densities (in thousands of individuals) of *Tetrahymena* in corresponding dendritic (a) and linear (b) landscapes at the end of the experiment (day 15) and across the three replicate landscapes. In these landscapes, outer nodes are labelled “O,” inner and central nodes are labelled “I” and “C”, respectively. [Colour figure can be viewed at wileyonlinelibrary.com]

2 | METHODS

2.1 | Study system

We use single-species protist microcosms to address the effect of spatial network structure on population dynamics and density patterns across space and time. Such protist microcosm experiments have a long history in ecology and evolution (Altermatt et al., 2015; Gause, 1934), and allow to causally disentangle drivers of ecological and/or evolutionary dynamics (e.g. Fjerdingstad, Schtickzelle, Manhes, Gutierrez & Clobert, 2007; Fronhofer & Altermatt, 2015; Giometto et al., 2014).

For our experiments, we used the bacterivorous ciliate species *T. pyriformis* as a model organism. It has a body length and body volume of about 35 μm and 1,400 μm^3 respectively (Giometto, Altermatt, Carrara, Maritan & Rinaldo, 2013), high growth rates ($2 < r_0 < 4/\text{day}$) and equilibrium densities ($6,000 < K < 15,000/\text{ml}$) (Fronhofer, Kropf & Altermatt, 2015), making it an ideal study organism to address population dynamics over short time periods including many generations. All experiments were conducted using a standard protist-culturing medium made from protist pellets (0.46 g/L; Carolina Biological Supply) and inoculated with three different species of freshwater bacteria (*Serratia fonticola*, *Bacillus subtilis* and *Brevibacillus brevis*). The nutrient medium was autoclaved and inoculated with 5% of a dense, about 1-week old culture of these bacteria. The protists (*Tetrahymena*) use these bacteria as resources. All organisms used in the experiment are heterotrophic, but experiments were nevertheless conducted under constant light at 20°C to a priori avoid any photoperiodic effects (for further details see Altermatt et al., 2015). Importantly, the nutrient medium used in the experiment was added at identical concentration to all patches at the

TABLE 1 Theoretical expectation of the distribution of densities in dendritic and linear networks (Figure 1) based solely on the assumption of active dispersal and the network’s connectivity pattern. Initially, patches are assumed to have K individuals. Patches lose all their emigrants (dK ; d being the dispersal rate), which are distributed equally to connecting patches. Patches will receive a fraction of the emigrants from connecting patches. For example, due to an edge effect, an outer patch in a dendritic landscape will lose dK emigrants and only receive $\frac{1}{3}dK$ immigrants from a connecting inner patch, as inner patches distribute their emigrants over 3 vertices. Note that we here neglect the effect of dispersal mortality (Bonte et al., 2012), as dispersal related mortality is likely very low in our experimental systems

	Linear	Dendritic
Outer	$\left(1 - \frac{1}{2}d\right)K$	$\left(1 - \frac{2}{3}d\right)K$
Inner	$\left(1 + \frac{1}{2}d\right)K$	$\left(1 + \frac{4}{3}d\right)K$
Central	K	K

onset of the experiment, that is, all patches had strictly identical starting conditions and subsequent differences cannot be attributed to initial differences. Abiotic resources (i.e. nutrients) were not replenished subsequently during the experiment (contrary to chemostat experiments). Thus, nutrients were depleted over the experiment by bacteria, which themselves were fed on by *Tetrahymena*.

2.2 | Experimental design

We constructed replicated linear and dendritic landscape networks of identical total patch and landscape volume (i.e. regional habitat capacity) and total length of connecting corridors, arranged according to the respective network structure (i.e. linear versus dendritic, Figure 1; three replicated landscapes per network type). Networks were constructed using 20 ml Sarstedt vials (Sarstedt, Nümbrecht, Germany), which were connected with silicone tubes (silicone tube inner $\varnothing = 4$ mm; VWR, Radnor, U.S.A.). Stopcocks (Discofix, B. Braun, Sempach, Switzerland) allowed us to control dispersal. The distance of each connecting tube including the stopcock was 6 cm. During all handling and sampling of the landscapes, stopcocks were closed such that there was no exchange of individuals due to the handling.

We filled the landscapes with 15 ml of medium, and inserted protists at equilibrium density (c. 1 week old cultures) at the onset of the experiment. We then allowed dispersal of protists three times per week (Monday, Wednesday, Friday) during 4 hr. This dispersal scenario was chosen based on extensive previous knowledge (Fronhofer & Altermatt, 2015; Fronhofer et al., 2017), showing that with a 4 hr dispersal period we have dispersal rates of approximately 5%–20% of the respective population. Thereby, population growth rates, intraspecific competition and dispersal across the landscapes were interacting and driving population dynamics and density distribution at the metapopulation scale. As all factors other than network configuration (linear versus dendritic) were kept constant, we can causally address the effect of landscape networks structure on spatiotemporal population dynamics. All 60 microcosms were sampled at day 0, 8 and 15 of the experiment to assess protist population densities and movement behaviour.

2.3 | Data collection

We assessed density as well as movement behaviour of protists using microscopy combined with automated video analysis using the free image analysis software IMAGEJ (version 1.46a; U.S. National Institutes of Health, Bethesda, MD, U.S.A., <http://imagej.nih.gov/ij/>) following the protocol by Pennekamp and Schtickzelle (2013). Specifically, per sampling event, we sampled 0.5 ml of each population replicate, and placed it in a counting cell chamber (total volume assessed per sample was 19 μ l, height of chamber 0.5 mm) under a Nikon SMZ1500 stereo-microscope (Nikon Corporation, Kanagawa, Japan) at 30-fold magnification. Using a Hamamatsu Orca Flash 4 video camera (Hamamatsu Photonics K.K., Hamamatsu City, Japan), we then recorded 20 s videos (total of 500 frames) per sample. The

scripted image analysis determines in a first step the position of moving particles that fall into the size range 20–200 pixels (correspond to the range of sizes these organisms can have, see also Fronhofer, Kropf, et al., 2015). This is done by subtracting information on particles/pixels across all paired, subsequent frames per video, such that the difference between two subsequent image frames can be extracted (i.e. one gets a “difference image”). In a second step, the location of all these moving particles are relinked across all frames to get movement paths of all protists in the video. This linking procedure was done using the MOSAIC particle tracker plug-in (see also Fronhofer, Kropf, et al., 2015). Based on the output of these analyses, we extracted population sizes (i.e. density) of protists as well as velocities, turning angle distribution, and net distance travelled as our movement parameters for all individuals measured.

2.4 | Statistical analyses

All analyses were done using R version 3.3.3 (R Development Core Team, 2016) and data can be downloaded from Dryad (DOI: 10.5061/dryad.4588p). We analysed the data using linear mixed effects models incorporated in the package *nlme* (version 3.1-131) (Pinheiro et al., 2016). We ranked all possible models of the respective fixed effects including interactions based on the Akaike information criterion corrected for small sample sizes (AICc) and assessed explanatory potential using AICc weights. For model selection we used maximum likelihood (ML) estimates obtained by simulated annealing (optimiser of lme function set to “optim” and “SANN”) and the best fitting model was subsequently refit using REML. For the density analyses we used square-root transformed density data as the response variable. For the movement analyses we used log-transformed Euclidean distances as the response variable. We included network position (central versus inner versus outer nodes; see Figure 1), network type (linear versus dendritic) and time (days 0, 8 and 15) as fixed effects. We also included time as a pseudo-replicate within each landscape (unique landscape ID) as random effect, due to the repeated measures of individual replicate microcosms over time.

The analysis of density-dependent movement included population density in a linear, squared and cubed term as the relationship between movement, respectively, dispersal, and density is known to be nonlinear in *T. pyriformis* (Fronhofer, Kropf, et al., 2015). In this analysis “network” was also included as a fixed effect and the random effect structure included “time” nested in “network” and “position”.

As best models identified by the model selection procedure tended to have limited support if one considered AICc weights (see, e.g. Tables 2 and 4), we used full model averaging (R package “MuMIn”, version 1.15.6) to obtain a potentially less biased model fits. Note that our conclusions are not affected by the specifics of our statistical analysis, as the main effects we report can be found regardless of model averaging. In order to keep the analyses of population densities and movement comparable, we used population

TABLE 2 Linear mixed model selection and averaging based on ΔAICc and AICc weights (W_{AICc}) for square-root transformed density data and models fitted using ML (see Figure 2 for a visualisation). “Time” is a continuous variable and includes measurements on day 0, 8 and 15; “position” is a factor capturing whether densities were measured in central, inner or outer patches (see Figure 1); “network” is a factor capturing whether densities were measured in linear or dendritic landscapes. The random effect structure is “time” nested in “landscape ID.” Model components and corresponding codes are: time (1), network (2), position (3), time:network (4), time:position (5), network:position (6), time:network:position (7)

Model components	df	ΔAICc	W_{AICc}
1, 2, 3, 4, 5, 6, 7	16	0	0.44
1, 2, 3, 4, 6	12	0.78	0.30
1, 2, 3, 4, 5, 6	14	2.40	0.13
1, 2, 3, 6	11	3.54	0.07
1, 2, 3, 5, 6	13	4.92	0.04
2, 3, 6	10	7.05	0.01
1, 2, 3, 4	10	9.28	0
1, 2, 3, 4, 5	12	10.78	0
1, 2, 3	9	12.08	0
1, 2, 3, 5	11	13.36	0
2, 3	8	15.65	0
1, 2, 4	8	15.90	0
1, 2	7	18.76	0
1, 3	8	22.19	0
2	6	22.38	0
1, 3, 5	10	23.53	0
3	7	25.68	0
1	6	28.45	0
Null model	5	32.00	0

level means of the movement data, which leads to conservative analyses and makes our findings more robust.

In order to compare variation in population densities between dendritic and linear landscapes, we used the ratio between interquartile ranges (IQR) and medians of the respective population densities. This measure is analogous to the coefficient of variation, but more robust with regards to the distribution of the underlying data. We analysed the difference between IQR/median obtained from linear and dendritic landscapes statistically using resampling (200,000 draws and random assignment to either linear or dendritic) and a one-sided test, as the theoretical prediction is that dendritic landscapes should exhibit higher variation in population densities than linear landscapes (distribution reported in Figure 4).

2.5 | Fitting theoretical expectations to data

In order to fit the theoretical expectations summarised in Table 1 to the observed population density data (only data from day 15) we used the Levenberg-Marquardt nonlinear least-squares algorithm (R package “minpack.lm”, version 1.2-1). The function *nls.lm* minimises the residuals between predicted and observed data. We compared two approaches: (1) fitting the models assuming identical d and K values for dendritic and linear landscapes and (2) allowing for landscape-specific d and K estimates. These two models were compared using AICc . Population density estimates were calculated using the fitted d and K values and the relationships shown in Table 1. Confidence intervals were calculated using the standard error estimates provided by the summary of the *nls.lm* function and appropriate error propagation using the R package “propagate” (version 1.0-4).

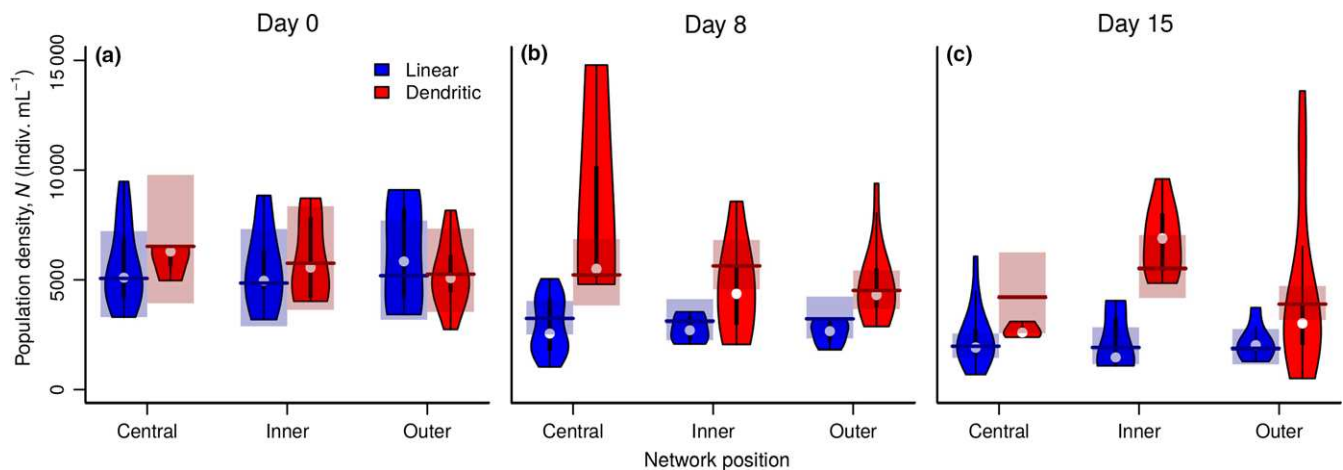


FIGURE 2 Distribution of *Tetrahymena* population densities depending on network type (linear versus dendritic networks), network position (central versus inner versus outer nodes) and time (days 0, 8 and 15). Violin plots show the overall distribution of the data, the white point gives the median, and the solid black line the 25% and 75% percentiles, respectively. Given the network structure (Figure 1) and the three replicates per landscape, distributions include $N = 18$ (9, 3) measurements for outer (inner, central) nodes of dendritic networks and $N = 6$ (6, 18) measurements for outer (inner, central) nodes of linear landscapes. Horizontal lines visualise back-transformed parameter estimates of the averaged linear mixed effects model and shaded areas show 95% confidence intervals (see Table 2 for model selection results). [Colour figure can be viewed at wileyonlinelibrary.com]

3 | RESULTS

At the end of the experiment (day 15; Figure 1), we observed differences in population densities between networks and, for dendritic networks, also within the network between different patch locations (central versus inner versus outer; Figures 1 and 2). These differences were captured quantitatively by the statistical models (Table 2). While the full model showed the best fit ($\Delta\text{AICc} = 0$), its support was somewhat ambiguous ($W_{\text{AICc}} = 0.44$). The fit of the averaged model (Figure 2) shows clear differences in densities between landscapes and within the dendritic landscape at the end of the experiment (day 15).

The observed differences in densities follow theoretical predictions to a large extent quantitatively (Table 1, Figure 3). Fitting the theoretical expectations summarised in Table 1 to the density data of day 15 allowed us to estimate dispersal rates (d) and carrying capacities (K) as well as compare data and model expectations. While fitting the expected densities of Table 1 to data from

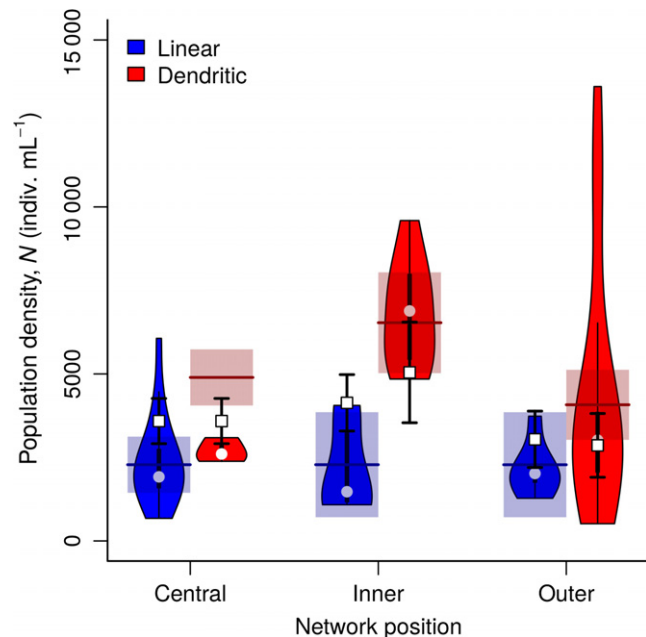


FIGURE 3 Fit of theoretical expectations to the distribution of *Tetrahymena* population densities depending on network type (linear versus dendritic networks), network position (central versus inner versus outer nodes) for day 15. Violin plots show the overall distribution of the data, the white point gives the median, and the solid black line the 25% and 75% percentiles, respectively. Given the network structure (Figure 1) and the three replicates per landscape, distributions include $N = 18$ (9, 3) measurements for outer (inner, central) nodes of dendritic networks and $N = 6$ (6, 18) measurements for outer (inner, central) nodes of linear landscapes. Horizontal red and blue lines visualise fits of the theoretically expected distribution of population densities to data from the dendritic and linear networks assuming network specific dispersal rates (d) and carrying capacities (K). White squares show fits of the theoretically expected distribution of population densities assuming the same d and K values for both network types. Shaded areas, respectively, error bars, show 95% confidence intervals of the fits. [Colour figure can be viewed at wileyonlinelibrary.com]

linear and dendritic landscapes assuming identical dispersal rates and carrying capacities across networks recaptured the empirical patterns qualitatively, fitting the expectations for linear and dendritic landscapes assuming network specific d and K values separately yielded a better fit between data and expectations regardless of the higher number of parameters ($\Delta\text{AICc} = 12.97$; Figure 3). While the joint fitting yielded an estimate of $d = 0.30$ (± 0.14) and of $K = 3,589$ (± 346 ; estimate \pm standard error), the landscape specific fits estimate higher dispersal rates and carrying capacities in the dendritic compared to the linear landscapes: $d_{\text{dendritic}} = 0.25$ (± 0.10), $K_{\text{dendritic}} = 4,896$ (± 429), $d_{\text{linear}} = 0.0005$ (± 0.59), $K_{\text{linear}} = 2,282$ (± 429).

Besides predicting a specific spatial distribution of densities in the different networks, our simplified theoretical expectations (Table 1) as well as current theoretical work (Fronhofer & Altermatt, 2017) predict higher variation in population densities within dendritic networks compared to linear landscapes. Our experimental data support these model predictions, as a conservative measure of variation (the IQR) standardised with the median of population densities showed a non-random deviation towards larger values in dendritic compared to linear landscapes (Figure 4).

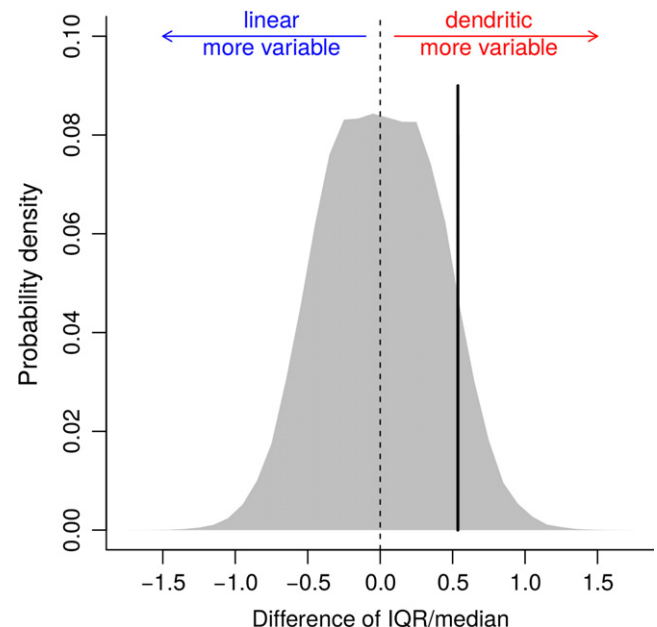


FIGURE 4 Comparison of variation in population densities between linear and dendritic networks at day 15 of the experiment. The solid line represents the difference between inter-quartile range (IQR) over median population densities of linear and dendritic landscapes. The distribution (grey) represents the distribution of the differences between IQR over median population densities of 200,000 random re-samplings for our data. As we theoretically expect the dendritic landscapes to be more variable we can perform a one-sided test which gives a probability of $p = .047$ of our observed difference between IQR to median ratios to be larger than zero. [Colour figure can be viewed at wileyonlinelibrary.com]

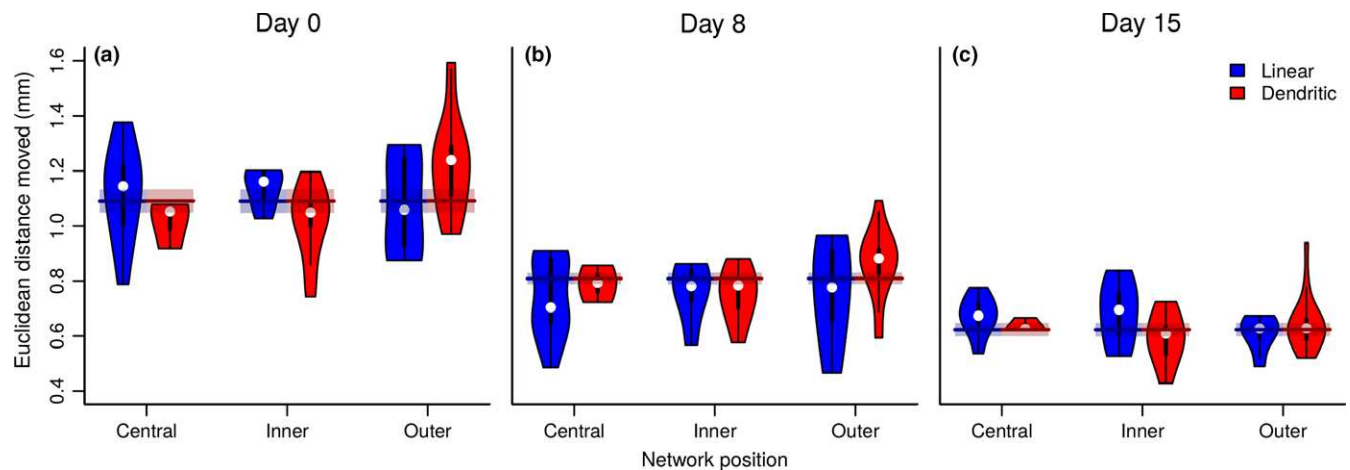


FIGURE 5 Euclidean distances moved by *Tetrahymena* individuals depending on network type (linear versus dendritic networks), network position (central versus inner versus outer nodes) and time (days 0, 8 and 15). Violin plots show the overall distribution of the data, the white point gives the median, and the solid black line the 25% and 75% percentiles, respectively. Given the network structure (Figure 1) and the three replicates per landscape distributions include $N = 18$ (9, 3) measurements for outer (inner, central) nodes of dendritic networks and $N = 6$ (6, 18) measurements for outer (inner, central) nodes of linear landscapes. Horizontal lines visualise back-transformed parameter estimates of the averaged linear mixed effects model and shaded areas show 95% confidence intervals (see Table 3 for model selection results). [Colour figure can be viewed at wileyonlinelibrary.com]

While we did not find differences in movement between patches or landscapes (Figure 5, Table 3), we did find an overall positive density dependence of movement (Figure 6, Table 4).

4 | DISCUSSION

We experimentally demonstrated that differing network configurations, specifically dendritic versus linear networks, can result in different spatial density distributions of single-species populations in otherwise completely homogeneous environments (Figures 1–4) both across these networks (dendritic versus linear) as well as within these networks (central versus outer versus inner nodes). Thereby, the dendritic network structure and dispersal therein have a direct effect on the population dynamics and structure of the spatially structured population (metapopulation *sensu lato*). This ecological consequence of dispersal in differently structured networks, that is, the dependence of density on network position and connectivity, is the precondition for subsequent evolutionary dynamics predicted to occur in networks of differing connectivity (Fronhofer & Altermatt, 2017; Henriques-Silva et al., 2015). Remarkably, we observe these differences despite (weakly) density-dependent movement (Figure 6), which is supposed to homogenise population densities across a landscape.

The effect of network structure on community dynamics and occurrence of organisms has been extensively studied, with a strong recent focus on particular network types, such as dendritic riverine networks (e.g. Carrara et al., 2012; Grant et al., 2007; Mari et al., 2014; Muneeppeerakul et al., 2008; Peterson et al., 2013; Seymour et al., 2015). In all of these studies, the occurrence of organisms in individual patches/nodes within the network

has been linked to network position, and a dependency of genetic structure and evolutionary dynamics due to network structure has been theoretically predicted (e.g. Fronhofer & Altermatt, 2017; Henriques-Silva et al., 2015; Labonne, Ravigné, Parisi & Gaucherel, 2008; Paz-Vinas & Blanchet, 2015; Paz-Vinas, Loot, Stevens & Blanchet, 2015). While these studies include population dynamics, which subsequently affect extinction risks (Fagan, 2002; Fronhofer & Altermatt, 2017), the direct effect of network connectivity and network topology on population dynamics has been largely ignored experimentally. To our knowledge, our study is the first experimental demonstration of a direct effect of network structure and position on population densities. Specifically, we find more variable population densities in dendritic compared to linear networks (Figure 4), with inner nodes of these dendritic networks exhibiting increased population sizes (Figures 1 and 2) as predicted by theory (Table 1 and Figure 3). Our landscapes were of identical overall environmental conditions, and local patches only differed in their connectivity. Thus, the difference in population densities is a direct and inherent consequence of active dispersal across different connectivity driving ecological population dynamics of our study organism *Tetrahymena*.

Although all patches had the same initial resource availability, subsequent decreases in resources due to consumption by bacteria and protists, may lead to emergent variation in resource availability. While we do observe a general decrease of population densities over time (Figure 2, Table 2; likely as a consequence of resource depletion), importantly, the difference in population densities we observed is still ultimately driven by the different network configuration.

Interestingly, our results suggest that dispersal rates and carrying capacities differ at the end of the experiment in dendritic versus linear networks (Figure 3). Most likely only overall densities differ, as

TABLE 3 Linear mixed model selection and averaging based on ΔAIC_c and AIC_c weights (W_{AIC_c}) for log transformed movement data (Euclidean distance moved) and model fitted using ML (for a visualisation see Figure 5). “Time” is a continuous variable and includes measurements on day 0, 8 and 15; “position” is a factor capturing whether movement was measured in central, inner or outer patches (see Figure 1); “network” is a factor capturing whether movement was measured in linear or dendritic landscapes. The random effect structure is “time” nested in “landscape ID”. Model components and corresponding codes are: time (1), network (2), position (3), time:network (4), time:position (5), network:position (6), time:network:position (7)

Model components	df	ΔAIC_c	W_{AIC_c}
1	6	0	0.96
1, 2	7	7	0.03
1, 3	8	9.45	0.01
1, 2, 3	9	16.80	0
1, 2, 4	8	17.16	0
Null model	5	18.82	0
1, 2, 3, 6	11	19.26	0
2	6	24.24	0
1, 2, 3, 4	10	26.97	0
3	7	27.53	0
1, 3, 5	10	28.67	0
1, 2, 3, 4, 6	12	29.06	0
2, 3	8	33.99	0
1, 2, 3, 5	11	35.71	0
2, 3, 6	10	36.15	0
1, 2, 3, 5, 6	13	38.09	0
1, 2, 3, 4, 5	12	46.78	0
1, 2, 3, 4, 5, 6	14	49.11	0
1, 2, 3, 4, 5, 6, 7	16	68.29	0

the errors of the dispersal rate estimates are rather large and clearly overlap. Our movement data also suggest no differences in movement between landscapes (Figure 5, Table 2). We can only speculate about the underlying mechanisms, but one possibility would be weak density regulation above K (convex population regulation function). Our theoretical predictions only consider one time step, respectively, that density regulation always resets population sizes to K . If this is not the case, differences in densities could potentially accumulate over time and lead to an increase in population densities.

The ecological and evolutionary consequences of the observed effect of connectivity on density are manifold. First, these observed differences in densities are the basis of subsequent evolutionary changes, such as evolutionary differences in dispersal rates in networks of different connectivities (Fronhofer & Altermatt, 2017; Henriques-Silva et al., 2015). These evolutionary differences may even feed back on the ecological dynamics of the entire spatially structured population and alter metapopulation dynamics (Fronhofer & Altermatt, 2017). Second, our single-species metapopulation study also shows an underlying mechanism of the observed lower species

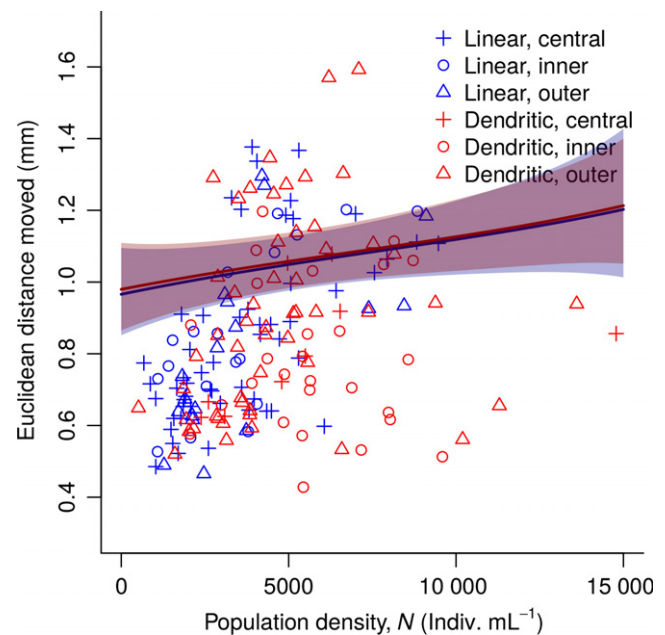


FIGURE 6 Euclidean distances moved by *Tetrahymena* individuals depending on densities in our entire dataset. Across all replicates of all landscapes (patches from different landscapes types highlighted by different symbols; see legend) we find positively density-dependent movement. The solid lines represent fits of the averaged linear mixed model (red: dendritic landscapes; blue: linear landscapes) and the shaded area shows 95% confidence intervals (see Table 4 for model selection results). [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 4 Linear mixed model selection and averaging based on ΔAIC_c and AIC_c weights (W_{AIC_c}) for log transformed movement data (Euclidean distance moved) as a function of density. Models were fitted using ML (for a visualisation see Figure 6). “Network” is a factor capturing whether movement was measured in linear or dendritic landscapes. “Density” is a continuous variable capturing the local population density in which movement was measured. The random effect structure is “time” nested in “network” and “position” (central, inner, outer; see Figure 1). Model components and corresponding codes are: density (1), network (2), squared density (3), cubed density (4), density:network (5), squared density:network (6), cubed density:network (7)

Model components	df	ΔAIC_c	W_{AIC_c}
1	9	0	0.42
1, 2	10	2.07	0.15
3	10	2.19	0.14
4	11	3.34	0.08
1, 2, 5	11	3.84	0.06
2, 3	11	4.27	0.05
Null model	8	4.28	0.05
2, 4	12	5.51	0.03
2	9	6.21	0.02
2, 3, 6	13	6.64	0.02
2, 4, 7	15	11.31	0

richness values in isolated headwaters both in real river networks (e.g. Altermatt et al., 2013; Heino et al., 2015; Liu et al., 2013; but see Besemer et al., 2013) as well as in experimental river-like networks (Carrara et al., 2012, 2014; Seymour & Altermatt, 2014; Seymour et al., 2015): the lower connectivity and thus reduced immigration have direct negative effects on local population densities, which eventually makes these populations more prone to extinction purely based on demographic stochasticity.

Our findings from a single-species metapopulation model system are also informative for multi-species metacommunities and the observed direct effect of network structure and position on population densities has important implications for the coexistence of multiple species. For example, the increased population densities in inner nodes of dendritic networks will reduce local population extinctions due to drift, and can thus be an underlying cause of a larger number of coexisting species at these nodes in dendritic metacommunities. However, this scenario assumes that species are not directly competing for the same resources and that densities of multiple species are not negatively correlated with each other. In the case of direct competition, the effect of dispersal and network position on higher local population persistence may be counteracted by increased competition of multiple species for the same resources. Thus, while we show for a single species how dispersal and network position affects population sizes, the subsequent community consequences will depend on the interplay between drift, species-specific dispersal and competition between the species (Vellend, 2010). Furthermore, dynamics in multi-species metacommunities will also be affected by a higher biological heterogeneity, as different species have different dispersal rates and dispersal distances, and may differently adjust their dispersal with respect to intra- and interspecific densities (Cote et al., 2017; Fronhofer, Klecka, Melian & Altermatt, 2015; Fronhofer, Kropf, et al., 2015).

In our experiments we also observed a dependency of movement (as a proxy of dispersal) on population density (Figure 6, Table 4) as in previous studies (Fronhofer, Kropf, et al., 2015; Pennekamp, Mitchell, Chaine & Schtickzelle, 2014). However, this effect was rather weak, as we did not find it space (Figure 5, Table 3). It is remarkable that we find the expected differences in population densities despite density-dependent movement, as density-dependent movement is supposed to homogenise densities across space. This underlines the strength of the effect of network structure on generating heterogeneity in population densities.

Our microcosm experiments were not designed to mimic a natural system in detail, but rather to test the significance of network structure in a causal way. Nevertheless, the observed patterns may guide our understanding of population dynamics in real river systems, as the studied network topologies can be seen as simple but realistic descriptions of real river networks (Altermatt, 2013). For example, it is a common phenomenon to find strong temporal but also spatial dynamics in population densities for many types of organisms in riverine ecosystems. These dynamics may also be seen in classic “bloom” phenomena of mass-emergences of certain aquatic invertebrates (e.g. mayflies) that can be found

in some riverine ecosystems. In the past, many of these spatiotemporal dynamics have been linked to local environmental conditions (for two recent examples, e.g. Heino et al., 2015; Kaelin & Altermatt, 2016). Our work shows that the specific position within a river network, and the dependency of local population dynamics shaped by spatially explicit topologies of neighbouring populations may be an additional mechanism generating variation in population abundances. Thus, tributaries may enhance the abundance of organisms at confluences and, as previously documented, also richness (Fernandes, Podos & Lundberg, 2004). As a consequence, fluctuations in population abundances due to the spatial position and connectivity of the respective population in the river network may affect species interactions and community dynamics, and influence higher level diversity metrics and metacommunity dynamics. Thus, our findings identify network topology as a possible additional mechanisms generating dynamics in population and community fluctuations in riverine organisms. The experimentally observed patterns are not only matching empirically observed patterns in real systems (Grant et al., 2007; Morrissey & De Kerckhove, 2009), but are also substantiating theoretical predictions. We thus think that the patterns are robust and of general significance. Our results highlight the importance of taking into account the explicit spatial structure of metapopulations and metacommunities for understanding population dynamics and dispersal strategies. While these findings do not preclude the significance of other environmental drivers on both the occurrence as well as the abundance of organisms in riverine networks, they indicate that some of the observed patterns, or at least some of the unexplained variation therein, may be driven by inherent characteristics of the dendritic networks themselves.

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DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.4588p>

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